Cranial Capacity and Performance on Delay-Response Task Correlated With Principal Sulcus Length in Monkeys

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ABSTRACT During the process of evolution, a selective advantage may have been gained by organisms that had the ability to utilize mentally stored information of a stimulus rather than the stimulus itself. The ability to temporarily store and mentally operate on stimulus information is often termed "working memory." Within the neocortex of primates, the functional anatomic subdivision surrounding the principal (rectus) sulcus plays an important role in modulating the performance of delay-response tasks in monkeys (representing working memory). However, it appears that no study has investigated the direct relationship between the length of the principal sulcus and performance on a delay-response task. Therefore, this paper investigates the relationships between principal sulcus length and performance on delay-response tasks. However, to control for the effect of overall brain size on this relationship, cranial capacity is analyzed with both principal sulcus length and delay-response performance. Results support a consistent and significant correlation between principal sulcus length and performance on delayed-response tasks in a variety of Old World and New World monkeys. Principal sulcus length is also significantly correlated with cranial capacity; however, cranial capacity is not significantly correlated with performance on delayed-response tasks. The results of this investigation provide a method for analyzing cranial capacity and working-memory abilities in select primates based on principal sulcus length, and may prove useful for interpreting endocasts in the primate fossil record. Am J Phys Anthropol 109:33–40.

Organisms that are neurologically capable of temporarily storing and mentally operating on stimulus information of "real-world" stimuli in order to make future choices possess working memory (i.e., the temporary storage of information in the brain). From an evolutionary perspective, the ability to make choices based on mentally stored stimuli, rather than on continual exposure to the stimuli themselves, is posited to be a major selective advantage.

The ability to use working memory for goal-based decisions is intimately tied to properties of the prefrontal cortex. In primates, the prefrontal cortex has been implicated in the regulation of a number of complex behaviors including, attention, synthetic reasoning and planning, spatial orientation, global personality features, and working memory (Brozoski et al., 1979; Fuster and Alexander, 1971; Jacobsen, 1936). It is not surprising, therefore, that the prefrontal cortex of the primate brain is highly differentiated, allowing for the regulation of a vari-

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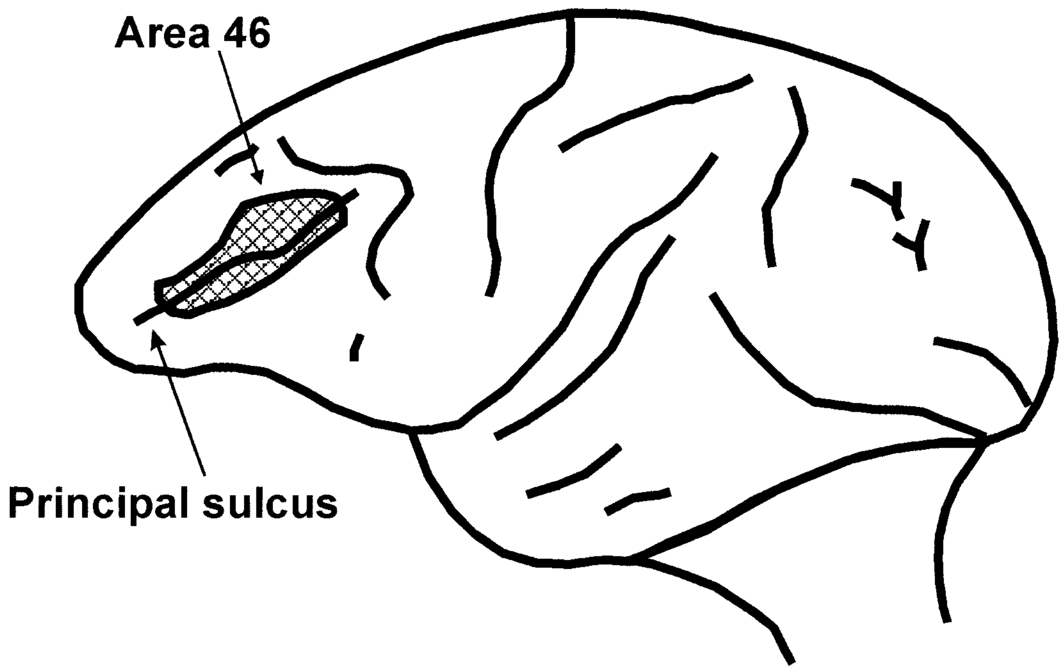

Fig. 1. Area 46 is situated around the principal sulcus in the monkey cerebral cortex (modified after Walker, 1940).

ety of behaviors via multiple functional-anatomic subdivisions (Goldman-Rakic, 1987). With recent advances in the neurosciences, a more definitive picture of the functional neuroanatomic properties of the prefrontal cortex is emerging.

One functional-anatomic subdivision demonstrated to be important in the processing of spatial working memory and performance on delay-response tasks in monkeys is the dorsolateral portion of the prefrontal cortex (Goldman and Rosvold, 1970; Goldman-Rakic, 1987; Sawaguchi and Goldman-Rakic, 1991). Historically, ablation studies of the 1930s, 1940s, and 1950s helped identify this general area of the prefrontal cortex as important for the regulation of working memory (Pribram, 1950; Mishkin, 1957). More recently, Levy and Goldman-Rakic (1997) were able to isolate functional area 46 (the area surrounding the principal (rectus) sulcus) as the specific cortical area involved in regulating performance on delay-response tasks in monkeys by selectively placing lesions to specific areas of the dorsolateral portion of the prefrontal cortex and testing subsequent performance (Fig. 1; modified after Walker, 1940). In humans, Courtney et al. (1998) showed spatial working memory to reside just superior and posterior to area 46 in the superior frontal sulcus of the cortex. They suggest that this shift in position of spatial working memory during primate brain evolution is the result of expansion in the anterior portions of the lateral prefrontal cortex, and may be related to the addition of new cognitive areas in humans. Consequently, this information helps explain the previously unrecognized homologous functional areas between humans and monkeys.

Delay-response tasks represent a subject's ability to hold information *on-line* (Sawaguchi and Goldman-Rakic, 1991; Williams and Goldman-Rakic, 1995). This means that during a delay-response task, working memory functions by mentally operating on a previously given stimulus, instead of on an ongoing exposure to the stimulus itself, to aid in decision-making processes. Put simply, the subject must remember the task at hand.

Most experimental delay-response procedures on non-human primates have subjects manipulate visual-spatial information, which the subject is required to remember in order to perform the task correctly. In a simple task, the subject is presented with either the reward (direct method) or an item that through conditioning comes to represent a reward (indirect method). These direct and indirect rewards are hidden in one of two locations. After a given period of time (delay), the subject is allowed to retrieve the item and a correct response results in a reward. The subsequent performance ability can then be assessed.

The *Diamond-Jane* strategy models behavioral functions across geological time by inferring behavior from comparative neuroanatomical data in extant species that have been experimentally tied to those behaviors (Masterton and Skeen, 1972). This strategy seeks to correlate specific structural changes in the brain with differences in behavioral performance. For that reason, this methodology is well-suited for formulating hypotheses about changes in behavior over time, and subsequently for aiding in phylogenetic interpretations about extinct fossil primates.

The principal sulcus appears in nearly all monkeys, and its length may be compared across primate species (Falk, 1978, 1979). Specifically, the principal sulcus courses through area 46, which is fundamentally related to carrying out delay-response activities (Goldman-Rakic, 1987). By applying the *Diamond-Jane* strategy to an analysis of area 46 in primates, it is reasonable to hypothesize that a correlation exists between the length of the principal sulcus and performance on delay-response tasks in monkeys. However, because increases in the general size of the brain as a whole may effect delay-response performance, overall brain size must also be considered (Finlay and Darlington, 1995; Gibson, 1998). Accordingly, the intent of this study was to investigate the relationships between principal sulcus length, performance ability on delay-response tasks, and cranial capacity in a variety of Old World and New World monkeys.

TABLE 1. Measured principal sulcus lengths and cranial capacities[1]

Primate genera	Principal sulcus length (cm)	Cranial capacity (cm^3)
Old World *Papio* (N = 5)	2.45	149
	1.91	140
	2.26	162
	2.48	197
	2.00	163
Mandrillus (N = 4)	2.18	152
	2.14	175
	1.55	136
	1.82	163
Macaca (N = 5)	1.67	92
	1.67	94
	1.72	106
	1.84	95
	1.83	99
Cercopithecus (N = 8)	0.65	67
	0.98	80
	1.18	64
	0.95	60
	1.10	82
	1.40	81
	1.35	84
	1.00	62
New World *Lagothrix* (N = 3)	1.18	95
	0.95	90
	0.98	103
Cebus (N = 5)	0.70	69
	0.84	—
	0.82	68
	1.11	70
	1.14	100

[1] Principal sulcus lengths are mean values of right and left sulci per specimen.

MATERIALS AND METHODS

Latex endocasts with corresponding cranial capacities representing four genera of Old World and two genera of New World primates were measured to determine principal sulcus length (Table 1). Only endocasts that reproduced good detail and were resilient enough to maintain their shape during measurement were included in the study. To determine principal sulcus length, a small piece of dental floss was aligned along the entire length of the principal sulcus, removed, straightened, and measured utilizing a sliding caliper.

Sample sizes ranged from 3–8 individuals per genus. Because t-tests of right and left hemispheres for the selected genera did not indicate any significant difference, both sides were included in the analysis. The final mean-length measurement was recorded as the principal sulcus size for each primate genus. Cranial capacities provided by Dean

TABLE 2. Computed scores and means of principal sulcus length, cranial capacity, and delay-response task performance[1]

Primate genera	PSL (cm) mean	CC (cm^3) mean	Delay-response score
Old World			
Papio	2.23	162	54
Mandrillus	1.92	157	44
Macaca	1.74	97	40
Cercopithecus	1.07	73	34
New World			
Lagothrix	1.03	96	23
Cebus	0.92	75	16

[1] PSL, principal sulcus length; CC, cranial capacity.

TABLE 3. Score conversions[1]

Percent correct	Score
100–96	10
95–91	9
90–86	8
85–81	7
80–76	6
75–71	5
70–66	4
65–61	3
60–56	2
55–51	1

[1] The mean percent correct scored by a genus in a given delay time is assigned the corresponding score. The scores are subsequently added across delay times to produce an overall score for that group.

Falk were obtained with mustard seed at the time the endocasts were cast (Falk, personal communication). A one-way analysis of variance (ANOVA) was applied to identify significance between genera in both principal sulcus length and cranial capacity. A regression analysis utilizing raw data was performed to determine the relationship between principal sulcus length and cranial capacity. Finally, correlation and regression analyses utilizing mean data were performed to investigate the relationship between performance on delay-response tasks with principal sulcus length and cranial capacity (Table 2).

Raw data for delay-response task performance was taken from two previously published studies (Harlow et al., 1932; Maslow and Harlow, 1932). Because solutions to delay-response tasks can utilize available spatial as well as nonspatial cues to cover the delay period, variations in delays between different studies of the same genus may be partly a function of methodology. However, performances can be compared in cases where studies used similar methodology (Michels and Brown, 1959).

Behavioral data were compiled for the genera listed in Table 1. Delay periods for task performance ranged from zero to greater than 180 sec, denoted by the following categories: 0, 5, 15, 30, 60, 120, and 180 (in sec). Within each primate genus, the percentage correct for each individual subject was recorded and averaged for each delay category. Since a comparison of overall ability was desired, an overall score was computed for each genus. Scores were calculated utilizing the scale in Table 3, where the percentage of correct responses for a given category was converted to the score for that category. Then the scores for each category were added up to represent the overall score for each genus. For example, if a genus averaged 95% correct responses for the 5-sec-delay category, then a score of 9 would be assigned. Subsequently, all category scores were added to equal the total score for each genus. Statistics used to analyze behavioral data consisted of a multivariate analysis of variance (MANOVA) for overall differences between genera across all times, and individual ANOVAs for between-genera differences at individual delay times.

RESULTS

In the analysis of delay-response performance, a single MANOVA across all delay times and including all genera was significant ($P < 0.05$). To further analyze delay-response performance, individual ANOVAs were calculated for each delay time between genera. Figure 2 shows delay-response performance plotted as an average percent correct across all delay times. Significance for delay times was found between genera at 5, 15, 30, and 60 sec ($P < 0.05$).

Differences between genera for both principal sulcus length and cranial capacity were evaluated using individual ANOVAs. For principal sulcus length differences between genera, a calculated F value of 88.8 was found significant at $P < 0.01$, with a critical F of 2.3. Likewise, differences between genera for cranial capacity produced a significant F value of 41.6, with critical F of 2.6 ($P < 0.01$).

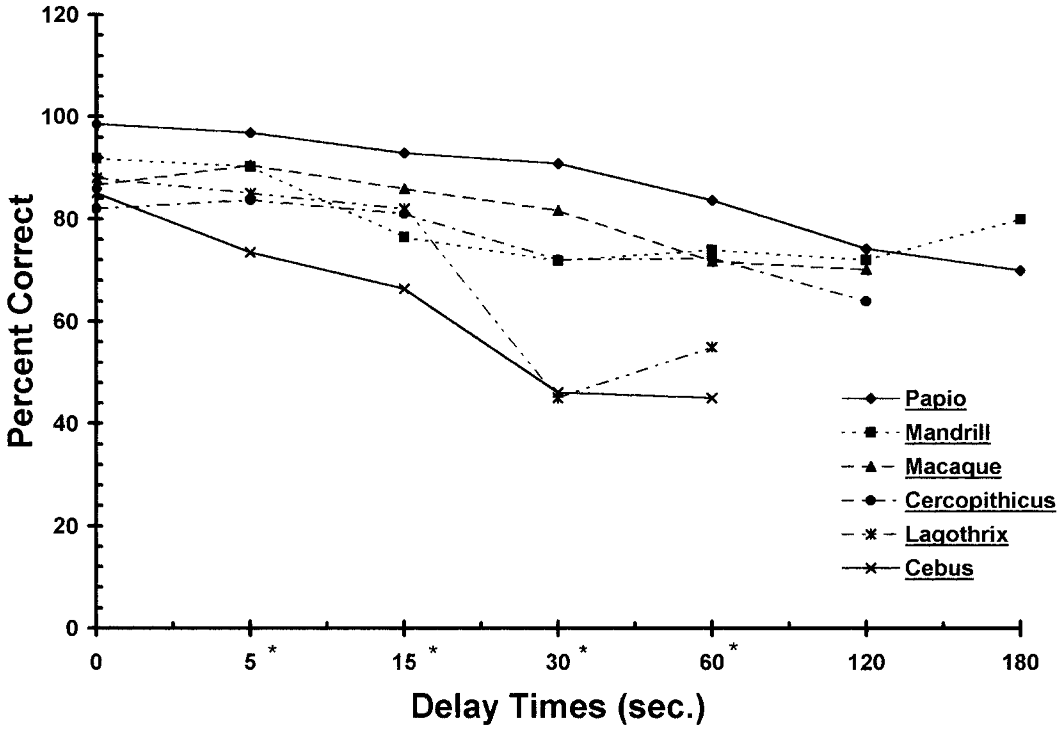

Fig. 2. Delay-response performance plotted as mean percent correct across delay times for all genera. *Denotes significant differences between genera for the delay times: 5, 15, 30, and 60 sec (ANOVA, $P < 0.05$).

The first regression analysis evaluated the relationship between principal sulcus length and cranial capacity. Plotting cranial capacity as a function of principal sulcus length produced a significant R^2 of 0.75 with a standard error of 20.0 ($P < 0.01$; Fig. 3). Next, to examine the relationship between principal sulcus length and delay-response task performance, a regression analysis plotting delay-response score as a function of principal sulcus length was utilized. The resulting calculation produced a significant R^2 of 0.88, with a standard error of 5.30 ($P < 0.01$; Fig. 4). Finally, a regression equation plotting delay-response score as a function of cranial capacity for each genus was calculated to judge the effect of overall brain size on delay-response task performance. A nonsignificant R^2 of 0.63 with a standard error of 9.5 resulted. However, because the computed correlation coefficient between cranial capacity and delay-response task score reached near-significance ($P < .06$), a test was conducted to control for the effect of overall brain size on the relationship between principal sulcus length and delay-response score. A partial correlation between principal sulcus length and delay-response score, controlling for cranial capacity, produced a significant correlation coefficient of 0.993 ($P < 0.01$). Correlation coefficients for the reported relationships are listed in Table 4.

DISCUSSION AND CONCLUSIONS

In monkeys, the ability to use working memory is intimately tied to the properties of the prefrontal cortex, and more specifically, to the area around the principal sulcus (Goldman-Rakic, 1987). The finding that principal sulcus length is significantly correlated with delay-response performance, while cranial capacity is not, may be due to the specific role of area 46 in keeping tasks *on-line* in higher primates. In fact, given the present state of knowledge about the localiza-

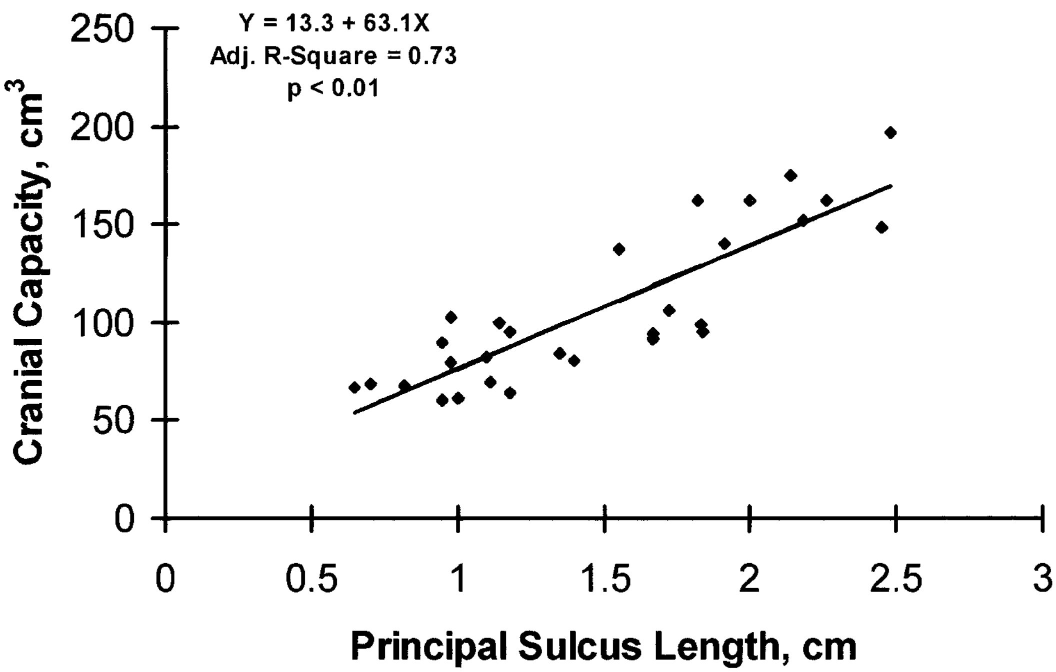

Fig. 3. Line fit plot of cranial capacity plotted as a function of principal sulcus length. Data points represent individual specimens.

tion of neurological substrates for delay-response performance relative to the principal sulcus, the stronger correlation observed between delay-response performance and principal sulcus length than with overall brain size is not particularly surprising (Bartley et al., 1997; Courtney et al., 1998). Because neurons along the principal sulcus are known to influence spatial working-memory ability, small increases in cortical tissue in this area may increase working-memory capacity. Conversely, small increases in overall brain size may have less direct effect on the size of the principal sulcus and, consequently, on working memory. Nevertheless, these results remain tentative. Ideally, an expanded study utilizing larger sample sizes representing a greater number of primate species, where principal sulcus lengths and brain sizes are measured using, for example, noninvasive medical imaging technology on the actual primates performing the delay-response task, would provide greater support for the reported relationships.

Without knowing the detailed neuronal workings of a variety of animal species (including humans), gross anatomical comparisons are compromised. However, certain behavioral tests have been devised, which, with ever-increasing accuracy and experimental manipulation, are able to establish strong correlations between functionally active brain regions and specific behaviors (Goldman-Rakic, 1987; Damasio et al., 1996; Carpenter et al., 1999). As the revolution in neuroscience continues, the level of precision in the identification of the neurological subdivisions responsible for specific behaviors enables the application of these findings to a variety of studies. Given that specific structural areas are related to specific behaviors (Smith and Jonides, 1999; Welker and Campos, 1963), it becomes possible to examine these correlations in light of phylogenetic relationships. Consequently, one may speculate that as a behavior becomes more complex over time, corresponding brain expansion of the area controlling that behavior should also increase.

One preliminary application of the present results permits an estimation of cranial capacity and ability on delay-response tasks

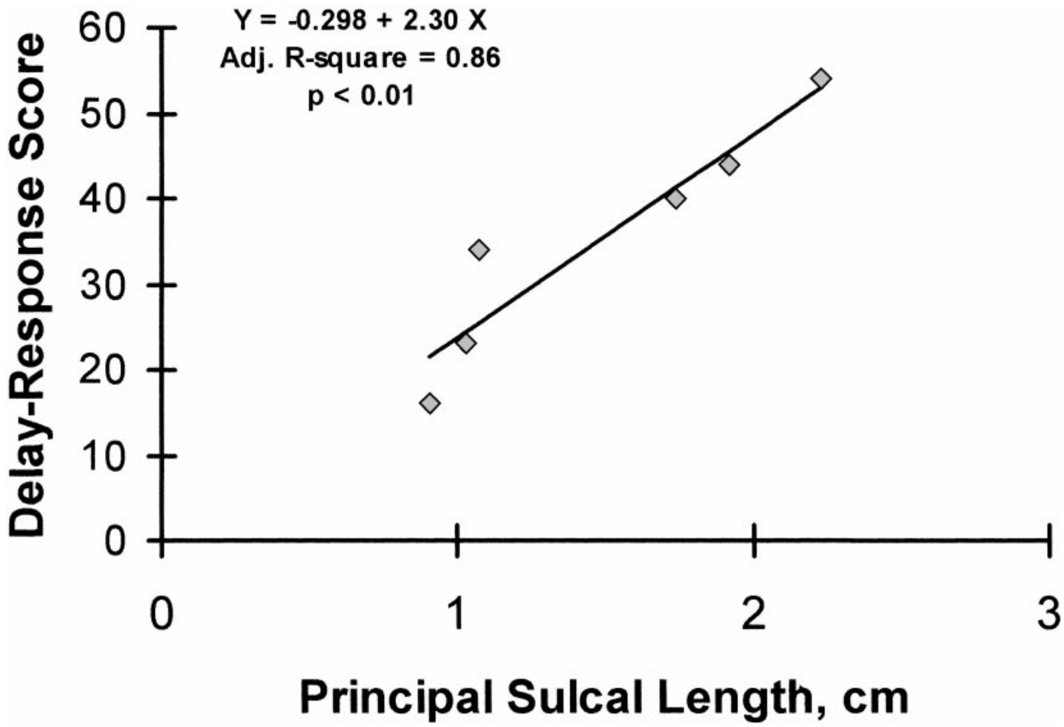

Fig. 4. Line fit plot of delay-response score plotted as a function of principal sulcus length. Data plots represent computed means for each genera.

TABLE 4. Correlations among principal sulcal lengths, delay-response scores, and cranial capacities[1]

Components	Correlation coefficient	*P* value
PSL Dly-rsp.	0.94	0.01
PSL CC	0.86	0.01
CC Dly-rsp.	0.80	0.06

[1] PSL, principal sulcus length; Dly-rsp., delay-response score; CC, cranial capacity.

in extinct fossil primates that exhibit similar brain morphologies. For example, *Dolichopithecus arvernensis* has been described as having a modern cercopithecine brain morphology similar to that of *Papio* (Radinsky, 1974). By measuring and inserting the principal sulcus length of this specimen into the regression equation for cranial capacity, a predicted cranial capacity value can be computed. Likewise, by plugging in the measured principal sulcus length into the regression equation for delay-response performance, a predicted delay-response performance score can be derived. When computed this way, *Dolichopithecus*' predicted cranial capacity is 152 cc, only 2 cc different from the 150 cc estimated by Radinsky (1974). The predicted delay-response score for *Dolichopithecus* is 50, implying a performance level at or above the level of *Papio.* Thus, these regression equations may prove useful for predicting cranial capacity and spatial working-memory abilities in other extinct primates that share similar brain morphology. Moreover, the length of the principal sulcus may prove useful in phylogenetic assessments of extinct primates where only a fragmentary fossil record is available.

The strategy of applying knowledge of the neuroanatomical bases that are known to underlie specific behaviors in higher primates will become more important in interpreting evolutionary changes in fossils as more knowledge of these structures comes to light. These data should facilitate the interpretation of the fossil record where specific differences in the abilities of our ancestors may be hypothetically identified, and assessed. Although working memory operates over seconds, its significance is delineated

over millennia. The differential abilities of primate genera to hold information *on-line* may help shed light on the evolutionary history of behavioral traits such as reasoning, and language comprehension (Wickelgren, 1997), and would therefore prove useful in the interpretation of proposed models of primate evolution.

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